

An Ecological and Behavioural Explanation of Mammalian Characteristics, and their Implication to Therapsid Evolution

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Introduction

The numerous differences which separate the generalized reptile from the generalized mammal have prompted a lively search for an explanation. It is assumed that mammalian characteristics arose from reptilian ones. This assumption appears to be acceptable, although ROMER (1968) cautions, and points to the early separation of the synapsids (that ultimately gave rise to mammals) from the reptilian stem. If synapsids diverged from other reptiles early in the Permian, then it is possible that the features typical of reptiles today are not representative of the early synapsids. This view is probably tenable if one compares details on the species level. However, the differences between generalized reptiles and mammals are mostly differences in degree, not kind, in which the reptilian condition is usually the simpler or more primitive. Thus the assumption that mammalian ancestors were similar in habits to reptiles of today is not really a bad one.

This paper is prompted by the recognition that principles emerging from the recent sciences of ecology and animal behaviour are applicable to extinct forms and permit new insights about the life from the past. Students of anatomy and paleontology have been quite cautious in interpreting form and function, at times unrealistically so. For instance, skulls are commonly explained in terms of feeding adaptations (i. e. FLEKOV 1965 for *Bison*). However, the skulls of ungulates must not only withstand the forces generated by masticatory muscles, but in most species also the great forces generated by head-on collisions, and wrestling with locked horns in combat. It is instructive to compare the skulls of related species with very similar food habits and habitat preferences, but different combat techniques. The mountain sheep (*Ovis*) and the mountain goat (*Oreamnos*) are good examples (see GEIST, 1971a). In a similar vein, a student of ecology and behaviour may find unconvincing HOPSON's (1969) and BARGHUSEN and HOPSON's (1970) viewpoint that the enlargement of the dentary, the development of mammalian-type adductor jaw musculature, and the subsequent evolution of the dentary-squamosal joint is primarily due to an increase in the dietary forces (mastication and prey capture). One can make a reasonable case for social selection being of some importance in producing the mammalian-type jaw. Although the forces imposed upon cynodont jaws during prey capture would be great, they would nevertheless be minor compared with the forces the lower jaws would have to withstand in the intraspecific combat as probably practiced by the cynodonts.

Let us assume that cynodonts used the same principles in combat that one can recognize in the combat behaviour of present-day vertebrates. One such principle is to deny the opponent the use of his weapons. This is achieved by grasping or, in some other manner, locking onto the weapon and hanging on, thereby frustrating the opponent's attempt to free his weapon for use. It was SCHENKEL (1967) who discovered that wolves grasp in combat the opponent's jaws and thus each prevents the other from using his teeth. It was pointed out by GEIST (1966, 1971) that ungulates in many

cases use the same principle, catching and locking onto each others' horns, frustrating their efficient use. Subsequent observations indicated that this is a widely practiced form of defence, and that many actions preceding combat are preparations to catch and hold those dangerous jaws, beaks, tusks or horns. Once the weapons are grasped a wrestling match develops in which the opponents attempt to free the weapons or hold on, respectively, resulting in great forces being applied to the weapons. In the present case, this would be the lower jaw. A lower jaw sufficient only for mastication is clearly inadequate to the animal unless it can withstand the forces of intraspecific combat--assuming the combatants grasp jaws.

Our assumption that cynodonts possessed frontal jaw grasping, and combat like modern carnivores, finds support in a number of therapsid attributes. Note the short tail of cynodonts i. e. *Thrinaxodon* (BRINK 1956) or even *Cynognathus*. In reptiles, the massive tails are used in inter- and intraspecific combat (ROTTER 1963, BELLAIRS 1969). A reduction in tail size and increase in the sturdiness of the skull and jaws suggest a shift of emphasis in combat from tail lashing to biting, and consequently a defence against biting, namely jaw grasping. This mode of defence could well have been practiced by the gorgonopsians i. e. *Lycaenops* (COLBERT 1958, Fig. 42). The exceedingly massive lower jaw of this genus may well have evolved to resist crushing when grasped, as well as to protect the long canines against breakage.

A shift from tail lashing to frontal combat is also indicated in other therapsid lineages. In the Dinocephalia and Dicynodontia there appears to be a relationship between jaw structures adapted to a herbivorous diet, thick-boned skulls, and horn-like bumps on the head, or tusks in the upper jaw. This indicates that therapsids did what a number of herbivores have done since: in the absence of a massive tail, and in possession of jaws devoid of a massive, strong hinge, they adapted by pushing each other in combat head on, and wrestling with locked horns and tusks. Following trends set by modern ungulates as guidelines, one would not be surprised if a close examination of the Anomodontia would reveal that each specialization in dentition is accompanied by an increase in size, number, or complexity of horn-like organs (GEIST 1971b). One should also find that the occiput and neck vertebrae should reflect the forces they are subjected to during butting and head wrestling. Ceratopsians also show an inverse relationship between the size of their tails and the size of their anterior combat organs (see COLBERT 1968).

Had dietary forces been responsible for the mammalian-type jaw, then it should have evolved in herbivores, not carnivores. That herbivorous therapsids, i. e. the *Tritylodontia* took advantage of the large dentary and new, highly-developed musculature to develop the rodent-like niche, is irrelevant to this argument. BARGHUSEN and HOPSON (1970) show that the mammalian-type jaw began in the carnivores. It is noteworthy that in ancient or modern herbivores which masticated and shredded fibrous plant tissue, i. e. Dicynodontia, the ceratopsians, hadrosaurs and modern ungulates, there is little evidence of a jaw joint of exceptional strength. The skulls of herbivorous Anomodontia indicate the former presence of massive adductor muscles, but no strong jaw joint or enlarged dentary as seen in cynodonts. Solid jaws and joints are found today mainly in carnivores, rather than herbivores (with some exceptions). These points also suggest that the evolution of a mammalian-type jaw, head musculature, and jaw articulation is related to greater forces than would be required by mastication. If prey capture was responsible for the evolution of strong jaws and jaw joints in cynodonts, why not in varanids, crocodylians, and many large snakes? The foregoing serves to illustrate only that views other than those of HOPSON and BARGHUSEN are not unreasonable at the present stage of knowledge. However, I do concur with them that the evolution of cuspid teeth and fine control over the movements of the jaw were probably due to selection for efficient mastication.

This discussion naturally leads on to the question: why should there have been a selection against massive tails, resulting in the rather modest tail size typical of most mammals? This is one characteristic not satisfactorily explained. Others are: the diphodont or monophodont condition of mammals; the reduction in phalange formula to 2, 3, 3, 3, 3; the predominance of olfactory lobes in the brain; the evolution of a complex middle ear; the excretion of nitrogenous waste at high osmotic concentration; the presence of odoriferous glands; and the evolution of maternal care. However these characteristics can be explained as being part of one adaptive complex, of which endothermy is also a part.

Numerous mammalian characteristics have been related to endothermy by various authors (BRINK 1956, OLSON 1959, VAN VALEN 1960, HEATH 1968, HOPSON 1969, REED 1960). There has been dissension, i. e. SIMPSON (1960), who in criticizing REED's (1960) views pointed out that most mammalian features had no established relationship to endothermy. BRINK (1956), VAN VALEN (1960) and HEATH (1968) argued convincingly to the contrary. They showed that endothermy could be regarded both as a *consequence* and the *cause* of adaptations leading from the reptilian to the mammalian condition. Thus BRINK (1956) related the loss of lumbar ribs to the evolution of diaphragm breathing, and it, in turn, as an adaptation towards endothermy. HEATH (1968) suggested that endothermy was the effect of a new mechanism to maintain muscle tonus. This mechanism in turn was the effect of the re-organization of the appendicular skeleton and musculature from the reptilian towards the mammalian condition. An effect of the new tonus mechanism was the increase in metabolic heat production. According to JANSKY (1962, cited by HEATH) this accounts for up to 30 per cent of the heat production in mammals. HEATH (1968) also related the evolution of the pyramidal motor system and the presence of pons in therapsids and mammals to the evolution of mammalian-type posture and gait. HEATH (1968) may have been correct in suggesting that selection for a new kind of gait resulted in endothermy, yet, as shall be shown later, the ecological niche selecting for the mammalian-type gait would also select for endothermy; the former is not possible without the latter.

An attempt to explain the evolution of mammal-like reptiles with a view to their ecology, has been made by OLSON (1959). He suggested that early therapsid evolution from the pelycosaurian stem was tied to a semi-aquatic life. He based his thoughts on carefully evaluated death-assemblages of which therapsids and pelycosaurians were a consistent part. He does not demonstrate, however, why selection for semi-aquatic life should be causally connected to mammalian characteristics. The presence of mammalian characteristics in aquatic therapsids does not in itself indicate that mammalian characteristics are dependent on an aquatic niche. It must be shown that given an ecological profession (or niche), mammalian characteristics must necessarily be selected for, and each step closer to mammalhood is an improvement in the adaptations required for that profession. Such a niche is described and discussed below. Moreover this hypothesis explains some aspects of therapsid radiation and extinction. Contrary to SIMPSON (1960) it indicates that therapsids arose repeatedly from *one* adaptive complex, regardless of their final specialization, as did the tertiary therian mammals rise from *one* adaptive complex, namely that of small carnivores and insectivores.

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Hypothesis

An ecological niche which would select for mammalian characteristics given a generalized reptile, is that of a *small, nocturnal, forest-dwelling carnivore and insectivore* with *generalized food habits* in a cool climate. One should visualize this small animal emerging after dusk and, protected by darkness from larger carnivores, going in search of cold-numbered insects, amphibians, reptiles, and the now-unguarded reptile nests. Unlike reptiles, it searches continuously for its food and thus moves about steadily and covers long distances; it stalks and surprises prey and does not lie in wait for it; it remains active for a long time and retreats into hiding during the day. This description applies of course only to the master of this ecological profession who is already equipped with mammalian characteristics. The "apprentice" in the cool Permian would do well to be active for a few hours at night; yet these few hours would be safe and rewarding hours. To a Permian reptile, living in temperate zones, nocturnalism offers safety from large — but during the night sluggish — reptilian predators, and a chance to exploit a food source that is incapacitated by night-time darkness and cool temperatures. The adaptations required to exploit this niche successfully also required a complete re-organization of the reptilian structure, physiology, and behaviour.

This hypothesis hinges on the condition that the climate of the Permian is like that described by KURTÉN (1968), that is was a period of cool climates, of mountain building and maybe minor glaciations. This would mean reduction of tropics to a narrow, equatorial zone, the existence of large belts of temperate and cold climates not unlike the present, and the shifting of climatic belts with glaciations. The Permian was also an age of radiation by insects.

Application of Hypothesis to Mammalian Characteristics

Nocturnal activity in forests or shrub communities with closed canopies requires a greater dependence upon olfactory, tactile, and acoustic senses than upon vision. The presence of large olfactory lobes and mammal-like turbinals in cynodonts of early Triassic age (BRINK 1956), argues for the presence of a keen olfactory sense (see MOULTON 1967). The presence of depressions on the maxillary could be interpreted as evidence for the presence of odoriferous glands, not only sebaceous or poisonous glands (see BRINK 1956, VAN VALEN 1960). Odoriferous glands showing sex and age variation in size and type of secretion would be advantageous in allowing unambiguous identification in the dark or for marking territories; they would be most useful in the ecological niche postulated.

There is some evidence for vibrissae in therapsids (BRINK 1956), although VAN VALEN (1960) cautions against embracing the evidence hastily, and there are numerous foramina above the canines which suggest well-eneruated lips. This evidence is in line with the argument for nocturnal activity. Long vibrissae on a sensitive snout in combination with a keen olfactory sense would assume chemotactile functions, eminently useful in sniffing and feeling out grubs, insects, and small prey at night. A keen olfactory sense would also warn of predators close by, while permitting the animal to follow its own scented trail system.

There is no evidence to suggest that the therapsid ear was more sensitive than those of present-day reptiles (HOPSON 1966). The advantage of the mammalian ear probably lies in its sensitivity to a greater range of frequencies (GRINNELL 1968). The convergent evolution of the mammalian-type inner ear in the protheria and theria (HOPSON 1966) argues in favour of its significance as an adaptation to nocturnalism.

The condition emphasizing olfaction, probably touch, and a lesser emphasis on vision, appears to have begun in therapsids and remains a condition typical of many mammals.

A small predator moving about in search of food, stalking it, and wandering long distances will require strong limbs and some endurance. The evolution of the typical mammalian mode of transportation would fulfill just that requirement and would explain the appendicular skeleton, the emphasis on red rather than white muscles in mammals, the appearance of the pons, and the new tonus mechanism in the muscles which, as a by-product, would increase metabolic heat production. This contribution of HEATH's (1968) was mentioned earlier. HEATH also related the somatotropically-organized sensory projections in the forebrain of mammals to this mode of locomotion; albeit in a less convincing manner. It is not evident why such organization should benefit mammals, but is absent in birds.

It is noteworthy that the Permian period in which therapsids showed their first radiation was an age of glaciation and mountain building. Apparently the early Triassic was also cool. There would have been sharp differences in the day- and night-time temperatures in temperate zones. This sets the stage for a predator to exploit the inability of insects, amphibians, and reptiles to remain active during the night; it would also present the predator with a problem to keep warm. This problem would be greater for a small animal with unfavourable surface-to-mass ratio.

We know that present-day varanids can attain high body temperatures during peaks of activity, and that they can raise body temperatures fast, but lose heat slowly (BARTHOLOMEW and TUCKER 1964). They can therefore regulate heat loss to some extent, probably through vasoconstriction. Bioenergetic considerations suggest that varanids could reduce facultative heat loss, and thus maintain high body temperature longer if they reduced their massive tail in size. This would reduce the surface-to-mass ratio considerably. A simple model makes this plain.

Let us take a cylinder 10 cm long by 4 cm in diameter, a cone 3 cm high with the same diameter and a cone 10 cm long and make an "animal" out of it, with a tail 10 cm long. This animal would have a length of 23 cm and a weight of 179.8 g, given specific gravity equal to one. Its surface area would be 213.3 cm². Let's keep the mass and diameter of this "animal" constant but reduce the tail length by half, making it taper to a cone 3 cm long in the rear. Our "animal" is now 18.3 cm long and has a surface area of 200.1 cm², a reduction of 6.2 per cent. This reduction in surface area would lead to considerable savings in heat in environments dictating high energy expenditures to keep the animal warm; it would be insignificant in warm environments. Since the rate of cooling a body is proportional to its surface area, clearly a reduction in the surface-to-mass ratio of the body could be an evolutionary goal. It would select, in our hypothetical nocturnal reptile in a cool environment, for a compact body, stubby tail, and short appendages. This is precisely what we find in therapsids.

Some of the most peculiar and successful of the therapsids were the Dicynodontia and Tapinocephalia of late Permian and Triassic times (ROMER 1966, 1968; COLBERT 1968). Reconstructions indicate that these herbivores had exceedingly compact body forms. Next to the Pleistocene glyptodonts these were the next best thing to walking spheres. These therapsids were large animals, and may have exceeded a thousand pounds live weight (COLBERT 1955). It is informative to calculate the temperature regimes these animals could have lived in, and in particular if their compact body form would have been helpful in conserving body heat.

We can do this by comparing a cow weighing 400 kg to a 400 kg dicynodont, such as the round, compact *Kannemeyria*. We will deprive the cow of hair in our calculations, and allow both animals a food intake of 250 kcal kg W^{0.73}/24 hours of

apparent digested energy. Such an intake is reached on good hay in ruminants and is not a particularly good diet. We will follow BLAXTER et al. (1966) in using conversion factors of 0.81 to convert apparent digested energy to metabolizable energy, and of 0.73 to convert metabolizable energy to heat. Using BRODY's (1945) formula to find surface area (S) for cattle, $S = 0.15 W^{0.56}$, where W is the weight in kg, we find that a 400 kg cow has a surface area of 4.33 m². A sphere of the same mass has a surface area of 2.60 m². Since evaporative heat loss is about 300 kcal/m²/24h, and the energy cost of warming food is about 250 kcal per day, our naked cow has about 2,335 kcal/m²/24h of heat energy to lose before it goes into negative energy balance.

The temperature at which the cow has used up all her food energy for keeping warm (T_n) can be calculated from the formula

$$T_n = 39 - I_T (H_n)$$

where 39 is the body temperature in °C, I_T is the total insulation in °C/m²/24h/Mcal, and H_n is the sensible heat loss (Mcal/m²/24h). This formula is adapted from BLAXTER and WAINMAN (1961). In our case, we calculate insulation in an environment without wind, with a background radiation similar to that of a pasture on a cloudy day. Using the formula of JOYCE et al. (1966) to calculate air insulation (I_A) we obtain for a naked cow 8.7 units/m²/24h. To this we must add tissue insulation which we will take as 7.0 units/m²/24h. (Tissue insulation is due to the animal's ability to vasoconstrict.) Total insulation is hence 15.7 units/m²/24h. Heat production, $H_n = 2.33$ Mcal. The critical temperature of a naked cow under the conditions indicated is 2.3°C.

We do not, of course, know the surface area of the dicynodont we chose; however, let us assume its surface-to-mass ratio was better than that of the cow, maybe of the order of 1.4 times that of a sphere of equal mass instead of 1.67 times, as for the cow. Given identical conditions the dicynodont would have a critical temperature of -5.5°C. The significance of this can be indicated in another fashion: at 2.3°C the dicynodont would need a food intake of only 204 kcal kg $W^{0.73}$ to stay alive instead of 250 kcal kg $W^{0.73}$ as needed by the cow, a saving of 18.4 per cent in food energy.

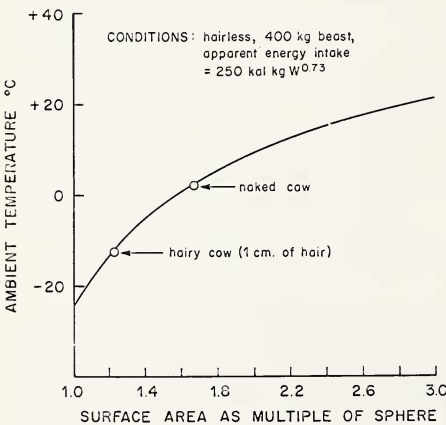


Fig. 1. Relationship between temperature at which endotherm goes into negative energy balance at a given energy intake, and its relative surface area. Considerable savings in energy can be attained by reducing relative surface area to 1.2 to 1.4, or by growing hair.

To show the effect of increasing roundness Figure 1 shows the critical temperatures of a 400 kg, hairless beast on an intake of 250 kcal kg $W^{0.73}$. Had the dicynodonts become perfect spheres the critical temperature would have dropped to -25.1°C. Clearly, energy can be saved by becoming more spherical in a cool environment, or conversely, it costs increasingly more to keep warm the more one deviates from perfect roundness. This is shown in Figure 2. It can be seen that somewhere between 2.0 and 2.5 times the area of a sphere, food intake required to keep warm at 0°C for a naked beast passes the 350 kcal kg $W^{0.73}$ mark. This is near the maximum feeding levels sheep can attain. Cattle may reach 400 kcal kg $W^{0.73}$, but this is very nearly the maximum energy intake possible. It evidently pays to deviate as little from a surface-to-mass ratio approaching a sphere as pos-

sible — unless one can grow a coat of hair. Thus a coat of only 1 cm thickness with an insulation value of $0.68^{\circ}\text{C}/\text{m}^2/\text{Mcal}/24\text{ h}/\text{mm}$ would raise total insulation (I_T) to 21.9°C , would drop the critical temperature (T_n) to -12.1°C , or at 2.3°C would save the cow 25.6 per cent in food energy compared to the naked condition. Clearly, a hair-coat is a far superior insulator to roundness. In our case 1 cm of haircoat is equivalent to about 0.5 units in roundness.

Nevertheless, the dicyonodonts and tapinocephalians could have lived in cool, or even cold climates without hair. If a layer of blubber could be added below the skin, then they could do even better in coping with cool temperatures while living off a more mediocre herbivorous diet than is indicated in Figure 1. Thus large size, compact body form, and some subcutaneous fat would have been ample to allow them to roam around in winters with snow on the ground, cold rain, and the occasional cold spell. If they had access to a diet superior in digestibility to hay, such as green vegetation, they could have maintained endothermy at temperatures lower still, probably as low as -25°C .

Assuming these creatures could have taken in $350\text{ kcal}/\text{kg}\text{ W}^{0.73}$ of apparent digested energy, then a 400 kg beast would require the intake of 2.4 liters of oxygen per minute, and ventilate about 100 liters of air per minute at standard temperatures and pressures. These figures assume a mammal-like capacity to extract oxygen from air. It is evident from this that the maximum rate of metabolism and heat production may well be limited by the lungs and circulatory system, as well as by the type and amount of food the animal can ingest.

Heat can, of course, also be conserved by choosing a habitat in which at night there is little radiation to the open sky. This can be achieved in the forest where a canopy provides a radiation shield (see MOEN 1968). A second advantage in choosing forest over open field would be the reduction in convective heat loss since winds are here reduced to a minimum. To a small, nocturnal animal in a cool environment the forest offers the best environment to minimize heat loss.

Should heat conservation be adaptive during daylight hours, when the animal is not active (and there is reason to suspect that this is so as explained below), heat can be conserved by huddling with a companion in a den or nest. This reduces the surface-to-mass ratio and appears to be a mechanism used by some snakes during hibernation (WHITE and LASIEWSKI 1971).

As has been illustrated, in the absence of an effective body covering of hair (or blubber), a high metabolic rate can be sustained only by a high rate of liberation of metabolizable energy. This energy must be offset by a ravenous appetite. We

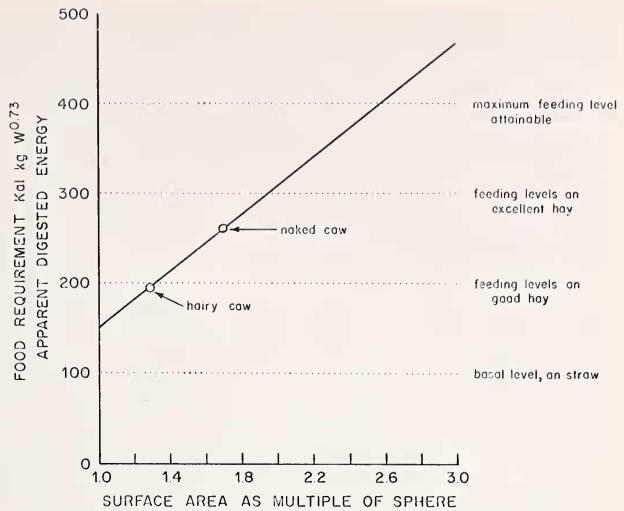


Fig. 2. Relationship between food intake required and relative surface area, to maintain endothermy at freezing point. In cold climates even large animals cannot realistically have a relative surface area larger than two.

find such to this very day in *Ornithorhynchus* (WALKER 1964), which, according to JOHANSEN (1962), does not possess well-regulated endothermy compared to therian mammals, or even echidna (SCHMIDT-NIELSEN et al. 1964). Such a system for maintaining body heat and activity depends on increasingly improving mechanisms to liberate energy from ingested food, for providing O₂, removing CO₂ and the breakdown products of nitrogen metabolism. It is likely that such a system evolved before a body covering of hair. It is useful to review the requirements for such a system since, in so doing, several characteristics typical of generalized mammals find an explanation.

The requirements are:

1. A rapid specialization towards selecting foods of a high caloric density, i. e. grubs, worms, insects, eggs, small vertebrates, and carrion. An added advantage of a high protein diet would be the heat increment generated beyond and above that of the existing heat production, provided the protein is catabolized for energy production and not the growth or replacement of tissues (BRODY 1945, KLEIBER 1961). Since the caloric effect of protein is higher than that of carbohydrates and fat, there would be an added gain in body heat for the resting animal, and a drop in the lower critical temperature.

2. A second requirement is a mechanism that fragments food to allow greater access to digestive enzymes, and hence a rapid liberation of metabolizable energy. Chewing and tearing the prey are such mechanisms. Originally chewing would do little more than puncture the prey's skin. This would allow nutritious body fluids to seep out and digestive juices to flow in. Mastication would select first for the codont teeth, then shearing cusps, crushing platforms, and finally multi-rooted teeth. It would produce a heterodont dentition. Simultaneously, as BOCK (1959) and BARGHUSEN and HOPSON (1970) have shown, there would be an increasing elaboration of mammalian-type musculature to move the jaws, and allow increasingly effective mastication. The evolution of a lower jaw consisting of one massive, flat jaw element on each side instead of a thin hollow tube made from several elements, should not be ascribed only to efficient mastication as pointed out earlier, but can also be related to intraspecific combat and the reduction of tail size and length. Hence the requirements of mastication, capture of prey, and intraspecific combat would collectively select for a massive skull with well-fused skull elements, heterodont dentition, and a strong jaw joint. Prey capture and intraspecific combat in particular would select against the prokinetic joints as found in many reptiles and birds. As BRINK (1956) points out, the palate may function primarily to separate food and air passages; secondarily, it would strengthen the skull.

3. As a consequence of high metabolic rate, the bloodstream is flooded with metabolic breakdown products. According to hypothesis the metabolic breakdown products are primarily due to protein digestion. This would flood the circulation with urea, raising the osmotic pressure, which in turn increases the flow of liquids into the circulatory system, and in turn puts strain on the heart and increases glomerular filtration rate, which in turn must be compensated by increased reabsorption of water and electrolytes unless the animal dehydrates. Hence, given selection for maintenance of high metabolic rate, there would be simultaneous selection for a larger heart, thicker arteries, and more efficient kidneys.

4. Urea is not the only breakdown product which must be removed; there is also a large amount of carbon dioxide. This can be removed only via an increased ventilation rate of the lungs and/or an increased lung area.

5. As has been pointed out repeatedly, a high metabolic rate requires a large amount of oxygen. To be more exact, a high concentration of O₂ is required in the arterial blood. This can be attained by increasing lung area and ventilation rate,

increasing the rate of perfusion of the lung with blood, and increasing the oxygen-carrying capacity of the blood. This means increasing the lung area per unit weight, achieved by the evolution of the alveolated lung. Since the cardiac output of mammals is higher than that of reptiles (WHITE 1968 a), it follows that the mammalian lungs are flushed with blood more rapidly. Furthermore, mammals have higher densities of erythrocytes in their blood than reptiles (HOAR 1966). Evidently selection for high metabolic activity would simultaneously also select for larger and complicated lungs, heavier and stronger hearts to force fluids through the increased capillary beds of the lungs, and an increased density of erythrocytes in the blood. The advantage of enucleated erythrocytes is not obvious.

6. Another manner of increasing oxygen intake and CO₂ excretion is to increase ventilation efficiency of the reptilian breathing system. In a "generalized" reptile, breathing is achieved by raising and lowering the ribs and increasing and decreasing the pleuro-peritoneal space (BRINK 1956, TEMPLETON and DAWSON 1963). In this system, gut space is critical. The lungs and the gut lie in the same cavity bordered by ribbed body walls. As was pointed out earlier, our hypothetical reptile--evolving into a nocturnal carnivore and insectivore--needs much food to maintain a high level of activity and has a ravenous appetite: consequently, its gut bulges. In the reptilian system the gut can expand, but only at the expense of the pleural space, and hence impaired breathing. Yet, both a high intake of food and a high intake of oxygen are selected for. The first requirement is hence to somehow prevent the gut from encroaching on the lungs and reducing ventilation. There is thus a need for a mechanism which holds the gut back. This was apparently achieved by the evolution of a tough septum which separated pleural from peritoneal cavity and contained the gut within the body cavity. This, however, left little room for the gut to expand--unless the lumbar ribs are shortened which allows the body to bulge out laterally and ventrally. But this opens the door for diaphragm breathing, in that if muscles enter the septum and allow contraction of the septum, the gut mass is pushed backward and the pleural cavity expands. A suspended gut-mass, unconfined by abdominal ribs, now becomes increasingly adaptive. The new system of breathing demands strong thoracic ribs lest the contraction of the diaphragm cause the ribs to move inward, reducing pleural space. The element allowing both increased food and oxygen intake is hence a suspended gut free to bulge out laterally and ventrally, thereby not interfering with the lungs, a diaphragm holding the gut back from the lungs and allowing an increase in ventilation by pushing the gut back, increasing pleural space, and a strong rib basket to counteract the forces of the diaphragm. This proposition differs from that of BRINK (1956) in that it proposes that evolution of diaphragm breathing became possible only *after* a substantial reduction in the length of lumbar ribs. It should be noted that in the interesting breathing mechanism of the crocodylians (see GANS 1970) the pleural cavity expands at the expense of the peritoneal cavity, when the liver is pulled back by the diaphragmaticus muscles. Breathing would become next to impossible for a crocodile should its gut bulge maximally with ingested food.

A maximally distended gut, even if it does not interfere with breathing, is a handicap during rapid movement; moreover, if selection does favour such an amassing of food per day, the gut contents have to be digested every day prior to the following nocturnal period of activity. In reptiles high body temperatures increase the speed of digestion and reptiles which have ingested food search out external heat sources (TEMPLETON 1970). A high body temperature maintained during nocturnal activity, as well as during the day, is probably essential for a complete digestion of each night's food supply. During the day heat gain can be obtained from external sources, much as reptiles gain it today. Nevertheless, this still leaves one problem to solve: How and where to store the digested energy? This can be done most conveniently by storing it

as fat, albeit at great energy costs, for lipogenesis is an expensive process (BLAXTER 1960). In a cool climate, however, the waste heat produced during lipogenesis (about 50 per cent of metabolizable energy) may not be wasted during the day if it makes the animal independent of an external heat source for maintaining a high body temperature to aid digestion. It would allow the animal to withdraw into cool hiding spots, such as burrows, and keep them warm with waste heat. In essence, in this system the animal moves about collecting food which is digested and the energy stored as fat to fuel the activity of the following day.

7. It is obvious that increased oxygen intake would be of little avail unless the oxygenated blood reaches the sites of high metabolic activity with a high load of oxygen. Evidently, diluting the oxygenated blood returning from the lungs with venous blood due to a three-chambered heart would reduce the favourable effects of increased lung surface and increased blood circulation. It is hence adaptive to the active animal to reduce the amount of venous and arterial blood mixing, or eliminate it entirely. Present-day reptiles and even amphibians and lungfish do have a good functional separation of arterial and venous blood (WHITE 1968b, JOHANSEN and HANSON 1968), but their circulatory systems do not work under such high pressures as those of mammals and birds, and an elimination of arterial and venous blood mixing could probably only be achieved via a four-chambered heart.

8. A consequence of enlarged lungs and kidney would be an increase in the capillary beds of these organs and, hence, an increase in friction for the heart to pump against. Clearly, it becomes adaptive to reduce excessive tubing elsewhere in the body and simplify the circulation system to reduce the workload for the heart. It is this which probably selected for the simplified circulatory system of mammals. It is not evident why the renal portal system is absent in mammals. Its absence cannot be related to the need of reducing the amount of "tubing" in the body, since the same requirement would apply to birds which possess a renal portal system.

9. A reduction of phalangeal joints and strengthening of the phalanges to carry the animal's weight would be a probable product of quadrupedal locomotion, and may be the indirect effect of a selection for compact body form. It has been pointed out by DAVIS (1964) in his work on the great panda that we need not postulate selection for every small change; some changes can be a secondary consequence. For instance, regard the silly correlation between an increase in horn-like organs in ungulates and the simultaneous reduction in the size of the tail (GEIST 1971b). It appears as though the animal's rear fell victim to expanded growth processes in the front, and the tail--in the absence of selection for large size--became smaller. Maybe phalanges became victims of growth priorities in the shoulder girdle. Moreover, as will be considered under maternal behaviour, there is reason to suspect that the ecological niche specified would also select for burrowing. This would also select for stronger phalanges.

10. A reptile evolving into a nocturnal way of life in a cool climate finds itself in a peculiar position with respect to reproduction. If it is a forest dweller, its eggs are not likely to be incubated in the sun except on some sandy stretches of creek or river bank, and lake shore. This would limit its distribution drastically and would create continuous pressure for ulterior modes of egg incubation. By definition, our nocturnal reptile is small, hence incapable of collecting sufficient rotting leaves to allow the heat of fermentation to do the incubating. It could use the heat of its own body to incubate the eggs, but this would require digging a burrow or making a nest, and this again poses problems. The female must feed during incubation and leave the nest, allowing the eggs to cool. In a cool or cold climate this could be a severe disadvantage. The animals could form a pair-bond and incubate alternately. This, however, would be possible only by an enormous change in behavioural adaptations. It may be that

ovovivipary, vivipary or a marsupium would be easier to evolve than pair-bonding. It is noteworthy here that the Indian python incubates at essentially endothermic temperatures (HUTCHINSON et al. 1966). Since our nocturnal reptile is maintaining endothermic temperatures throughout the day, it is possible for it to incubate its own eggs within the oviduct: that is, become ovoviviparous.

Once the young are "born" another problem arises. If the young were to move out at once and begin living in the same niche as their parents, they would have to have better thermoregulatory and food gathering mechanisms than their parents, since they are subject to greater heat loss due to unfavourable surface-mass ratio. Clearly, this is a contradiction. Therefore the young need an external supply of heat and a steady supply of food. This they obtain either by staying in a nest or clinging to the maternal body, while the parent supplies food. However, providing for ravenous young means that the parent must hunt, stalk, move about, and expose itself to the cool night air far more than in providing simply for itself. This is a requirement new to the reptilian way of life, a requirement that selects for ever-improving mammalian characteristics. Furthermore, the young need some protection. The relatively small parent can provide this only by either building a birdlike nest in an inaccessible locality, or by burrowing deeply and making the nest thus inaccessible to large diurnal predators. The food to feed the young would probably consist of minced prey regurgitated to the young; thus, the young would not need a complicated dentition until they reached the size of adults and began the adult way of life. The data on tooth development in *Diademodon* by BRINK (1956) support this view. Given such a system of feeding the young, there would be strong selection for effective grinding teeth; there would be selection for cutting teeth only if the young were to be fed by milk at first.

11. The proposed ecological niche responsible for the evolution of mammalian characteristics also explains the reduction in the number of tooth generations as found in mammals. Increased muscular activity and increased metabolic rate hastens senescence and shortens life expectancy, be it in endotherms or ectotherms (BRODY 1945). Selection for strong, complex teeth--a by-product of selection for increased metabolic rate--probably extends the life expectancy of each tooth. Simultaneously, the animal's life expectancy decreases. In essence, the permanent teeth last longer than the effective or average reproductive span of the individual. Given a short life expectancy, the loss of teeth becomes a penalty to the individual and is selected against. The result is further extension of the useful life of each tooth generation, and a reduction in the number of tooth generations to the very minimum.

Discussion

The foregoing shows that mammalian characteristics can be regarded as adaptations -- or the consequences of adaptations -- to the niche of a nocturnal, small-bodied carnivore with generalized food habits evolving in a temperate climate. Such conditions appear to have existed in the Permian and Triassic. Given a generalized reptile, this new ecological profession would have selected for an active creature which could maintain a high body temperature, which consequently would have a short life expectancy, a short-tailed, compact body, external insulation, and strong jaws and skull with long-lasting heterodont teeth, and an increasingly effective circulatory, excretory and respiratory system to deal with the high oxygen and food demands of such an animal and the metabolic wastes this creates. A shift to nocturnalism dictated a shift towards emphasizing olfaction, audition and the tactile senses over vision, a condition still inherent to most mammals. New ways of orientating and recognizing conspecifics by

means of olfaction and specialized sound-emission became possible. New forms of combat and courtship became necessary, as did the intensive care of young until they were as large as their parents. This in turn required adults to provide above and beyond their daily needs, for the daily needs of one or several young. In short, this new ecological profession required a new structure, physiology, an behaviour.

Yet, this new or mammalian way of life is in no way inherently superior over that of reptiles. Even today there are more species of reptiles than mammals, numbering about 6,000 (BELLAIRES 1968) versus about 4,800 (KRUMBIEGEL 1954). Reptiles outnumber mammals, particularly in the tropics where endothermy is probably of no great advantage. There is no evidence of mammals out-competing reptiles at the end of the Cretaceous (COLBERT 1968). In fact, it took about ten million years after the extinction of the Archosauria before mammalian ecological equivalents of the large ruling reptiles appeared on earth. The success of therapsids during the Permian and Triassic can be explained by the hypothesis that an ability to thermoregulate — even an imperfect ability — gave them a competitive advantage over diapsids in the cool zones of the earth. The decline in the fortune of therapsids at the end of the Triassic can likewise be explained in part by the increase in world-wide temperatures, hence the spread of tropical zones and the concurrent disappearance of temperate belts. In the tropics they would have no conceivable advantage over the ectothermic diapsids, but would be handicapped by their exceedingly high maintenance costs. Thus TEMPLETON (1970) in a review of reptilian thermoregulation and bioenergetics shows that mammals of equal body weight to reptiles produce 2.5 to 6.6 times more heat during normal resting metabolism than do reptiles.

Given the conditions of wide-spread temperate and cool climate belts in late Permian and early to mid-Triassic times, reptiles with even a poorly developed ability to thermoregulate would have had an advantage in colonizing areas outside the tropics. Therapsid radiations — like the later radiations of therian mammals — probably originated from small, nocturnal reptiles with some thermoregulatory ability. Every increase in body size would enhance this ability and would allow such forms to break with their nocturnal niche, and become capable competitors of diurnal reptiles. They could invade vacant niches in temperate belts and increase in size and diversify. In essence, therapsids represent probably a radiation of cool-climate animals, which remained abundant as long as tropical climates were restricted. The “sails” of early Permian pelycosauria, which have been thought of as thermoregulatory organs (ROMER 1966) also fit into this picture. They could be interpreted, along with the compact, short-tailed body shape of the advanced anomodonts, and the later evolution of hair, as adaptations to maximize heat gain or conservation, to allow extended activity in cool climates.

Regardless of the radiations of large, diurnal and diverse therapsids there would be a core of small, nocturnal species following a carnivorous way of life and perfecting their adaptations towards their niche. This brought them increasingly closer to the mammalian condition. They probably gave rise to several radiations, each approaching the mammalian condition a little closer. When in late Triassic times the spread of warm climates and tropics eliminated the competitive advantage of large-bodied, diurnal therapsids and allowed diapsids to flourish in an unprecedented manner, the small, nocturnal specialists were the only remnant of a large group which grappled with the problems of life in cool climates. This view appears to fit the evidence.

Summary

The characteristics which separate the “generalized reptile” from the “generalized mammal” can be explained as adaptations, or consequences of adaptations, to the niche of a small-

bodied, forest-dwelling, nocturnal carnivore in a temperate climate. This niche selects for roaming about in search of food, which requires a high body temperature despite low ambient temperatures. These requirements select for gaits, limbs, and muscles capable of economical, sustained activity. Heat was conserved by evolving a compact body shape and reducing tail size to reduce the surface-to-mass ratio, as well as by selecting a habitat with a minimum of convective and radiative heat loss. An external insulation was another adaptation to serve this end. With imperfect mechanisms to conserve heat, high body temperatures (and thus activity) can only be maintained by a rapid liberation and oxidation of metabolizable energy. This selects for a ravenous appetite; an abdomen free to bulge without interfering with the pleural space; an enlarged respiratory, circulatory and excretory system to deal with the increased need for O₂ absorption as well as CO₂; and nitrogen excretion. These requirements resulted in the loss of lumbar ribs, a hanging gut unconfined by strong body walls, and a septum restraining the gut from rolling forward and reducing lung volume. The need for a high concentration of O₂ in the blood, in connection with a high-pressure circulatory system, resulted in separation of arterial and venous blood. The circulatory system was simplified and strengthened to pump blood through enlarged capillary beds in the lungs and the kidneys. Rapid digestion of ingested food was aided by shredding it, thus increasing the surface area to enzyme activity. This selected for heterodont teeth of strong construction and long life expectancy. The diphiodont and monophiodont conditions were assumed because the life expectancy of the individual shrank, and the life expectancy of each tooth generation increased. Since the tail became ineffective as a weapon, combat shifted to biting. This resulted in the application of a defence whereby opponents grasp each others jaws to prevent the use of teeth. This, together with prey capture and to a lesser extent mastication, selected for strong jaws capable of withstanding being crushed, strong adductor muscles, and a strong jaw joint. Herbivorous mammal-like reptiles assumed butting and wrestling with horn-like organs. Nocturnalism selected for an increase in olfactory, auditory, and tactile acuity over vision, a condition typical of most mammals. These considerations imply that during the cool Permian and early Triassic period, therapsids were probably capable of limited thermoregulation and had a competitive advantage over diurnal reptiles in temperate zones. This advantage disappeared with the increase in world temperatures during Triassic times and the reduction and loss of temperate zones, leading to an extinction of diurnal therapsids.

Zusammenfassung

Die Merkmale, welche „generalisierte Reptilien“ von generalisierten Säugetieren“ unterscheiden, können als Anpassungen — oder Folgen von Anpassungen — an eine Nische für kleine waldbewohnende, nächtliche Raubtiere in einem gemäßigten Klima aufgefaßt werden. Diese Nische selektiert auf eine aktive, ausgedehnte Suche nach Nahrung; dies erfordert hohe Körpertemperaturen trotz niedriger Umgebungstemperaturen. Diese Bedingungen erfordern entsprechende Fortbewegungsweisen — Extremitäten, Muskulatur-, die eine ökonomische, aber anhaltende Aktivität zulassen. Diese Körpertemperatur wurde aufrechterhalten durch Entwicklung einer kompakten Körpergestalt mit verkürztem Schwanz, um das Verhältnis Oberfläche/Volumen zu verkleinern; weiterhin durch Auswahl eines Biotops mit einem Minimum an convectivem und radiativem Wärmeverlust. Eine weitere zugehörige Adaptation war eine äußere Isolation. Mit unvollständigen Mechanismen der Wärmekonservierung können hohe Körpertemperaturen (damit die Aktivität) nur aufrechterhalten werden durch einen erhöhten Stoffwechsel. Das führt zur Selektion auf einen hohen Nahrungsverbrauch, auf eine dehnungsfähige Bauchhöhle, die aber die Brusthöhle nicht beeinflusst; weiterhin zur Selektion auf vergrößerte, leistungsfähigere Atem-, Kreislauf- und Exkretionssysteme. Das führte zum Verlust der Lumbalrippen, zur Entwicklung einer dehnungsfähigen Eingeweidehöhle, eines Septum, das ein Vorrollen der Eingeweide in den Brustraum verhindert. Die Notwendigkeit hoher Sauerstoffkonzentration im Blut und hohen Blutdrucks führte zur Trennung von venösem und arteriellem Blut. Das Kreislaufsystem wurde verstärkt und vereinfacht, um das Blut durch die vergrößerten kapillaren Systeme von Lungen und Nieren zu pumpen. Eine schnelle Verdauung der aufgenommenen Nahrung wurde verbessert durch intensive Zerkleinerung, dadurch Vergrößerung der Oberflächen für Enzymaktivitäten. Das führte zur Selektion auf ein heterodontes Gebiß von erheblicher Stärke und Lebensdauer. Die diphiodonten und monophiodonten Zustände wurden erworben in Zusammenhang mit verkürzter Lebenserwartung der Individuen und verlängerter Lebenserwartung der Zahngenerationen. Der Schwanz als Waffe wurde überflüssig, Kämpfe mit dem Gebiß durchgeführt. Das führte zum Erwerb einer Verteidigungsweise, bei der die Gegner nach den Kiefern des Rivalen schnappen, um den Einsatz der Zähne zu verhindern. Diese Tatsache in Zusammenhang mit Beutefang und reduzierten Kaubewegungen selektierte auf starke, haltbare Kiefer mit entsprechender Muskulatur, und zu einem kräftigen Kiefergelenk. Pflanzenfressende säugetierähnliche Reptilien

erwarben für ihre Kämpfe hornähnliche Strukturen. Die nächtliche Lebensweise förderte gegenüber dem Gesichtssinn, dem Geruchssinn, dem Gehörsinn; das ist typisch für die meisten Säuger. Diese Überlegungen führen zu der Auffassung, daß im kühlen Perm und der frühen Trias die Therapsiden wahrscheinlich in begrenztem Umfang eine Temperaturregulation besaßen; sie waren in gemäßigten Gebieten den Tagaktiven gegenüber im Vorteil. Dieser Vorteil aber verschwand mit der Temperaturzunahme in der Trias, d. h. mit dem Rückgang gemäßigter Zonen; das führte zum Aussterben der tagaktiven Therapsida.

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